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Environmental constraints of the invasive *Mnemiopsis leidyi* in Scandinavian waters

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Abstract

We studied the seasonal dynamics of the invasive ctenophore *Mnemiopsis leidyi* over its distribution range from Skagerrak into the Baltic Proper during 1 yr and related this to ambient physical and biological variables. The appearance of *M. leidyi* was sporadic in the Baltic Proper, with 60-fold lower abundance than in the Skagerrak and Kattegat (mean 0.02 individual m^{-3} and 1.16 individual m^{-3}, respectively). *M. leidyi* typically resided above the halocline (10–20 m depth), except in the Baltic Proper where they were found deeper. Smaller size classes were underrepresented in the Baltic Proper, indicating failed reproduction or high mortality of the younger life stages. Ninety percent of the *M. leidyi* were observed at salinities of 22–29 and 75% of the individuals in water masses warmer than 11°C, i.e., typical late summer to autumn temperatures. Results of a Generalized Additive Model (GAM) indicate that the spatio-temporal distribution of *M. leidyi* might be explained by advection of *M. leidyi* from the Skagerrak and Kattegat area to the Baltic Proper. We conclude that the low salinity (< 9) of the Baltic Proper is likely to restrict successful reproduction and establishment of *M. leidyi* and that the advection of individuals from higher saline source areas sustained the observed Baltic Proper occurrence.

Rapid population growth and tolerance to a wide range of environmental conditions are typical traits of successful invasive organisms (Lee and Gelembiuk 2008). These traits characterize the ctenophore *Mnemiopsis leidyi*, which is considered a notorious invasive species, having invaded a wide range of novel habitats (Costello et al. 2012). *M. leidyi* has a wide latitudinal native occurrence, extending along the North American Atlantic coast (Purcell et al. 2001) and further south along the Argentinean coastline (Schaber et al. 2011). It was first introduced, presumably via ballast water, into the Black Sea in 1982 (Shiganova et al. 2001), later into the eastern Mediterranean and Caspian Seas (Ivanov et al. 2000), and more recently into the North and Baltic Seas (Javidpour et al. 2006; Boersma et al. 2007) as well as into the western Mediterranean Sea (Shiganova and Malej 2008; Fuentes et al. 2009). The invasion throughout Eurasian coastal waters has generated public, political, and scientific attention due to its potential ecological and environmental effects by disrupting ecosystems through its vast predatory potential (Kideys 2002).

In its native and exotic habitats, *M. leidyi* tolerates wide ranges of temperature and salinity (Fig. 1; Table 1), and it can also withstand low oxygen levels (Kolesar et al. 2010). As a simultaneous hermaphrodite with direct development from egg to tentaculate cydippid stage, followed by a transitional stage during which it gradually turns into an efficiently feeding adult lobate ctenophore (Sullivan and Gifford 2004), *M. leidyi* may rapidly grow and reach high numbers during favorable conditions (Purcell et al. 2001). The typical seasonal abundance pattern in temperate regions suggests a positive relation with temperature, reflecting that growth and egg production (Costello et al. 2006) increase with temperature. Salinity effects are less studied, but *M. leidyi* appears to have a wide salinity tolerance, depending on population (Fig. 1; Table 1). Nevertheless, egg production has been shown to be substantially suppressed under low salinities (< 10), which may constrain *M. leidyi* in the Baltic Sea (Jaspers et al. 2011). *M. leidyi* feeds omnivorously throughout its life (Sullivan and Gifford 2004). Tentaculate larvae capture nano- and microplankton (Sullivan and Gifford 2004), and lobate adults entrain mesozooplankton and ichtyoplankton in a feeding current (Purcell et al. 2001). Turbulence may directly interfere with feeding behavior and also affect vertical position through downward mixing (Miller 1974; Schaber et al. 2011). Also, vertically stratified waters seem to contain higher abundances than unstratified ones (Mianzan et al. 2010).

In Scandinavian waters *M. leidyi* was first observed in 2005 in the Oslo fjord (Oliveira 2007) and a year later in Skagerrak, Kattegat, and the Baltic Proper (Hansson 2006; Javidpour et al. 2006), and adult *M. leidyi* have been observed as far as the Gulf of Gdańsk in the southern Baltic Proper (Janas and Zgrundo 2007). A pronounced salinity gradient with a permanent stratification characterizes the Skagerrak, Kattegat, and Baltic Sea, where brackish, northward-flowing water from the Baltic Sea gradually mixes with the deeper and saltier southward-flowing North Sea water. The permanent density-driven water exchange is restricted by the shallow Danish straits (Great Belt and the Sound, Fig. 2), and larger saltwater inflows occur irregularly on a decadal timescale (Reissmann et al. 2009). However, inflowing salt water is known to bring saltwater species each year into the species-poor

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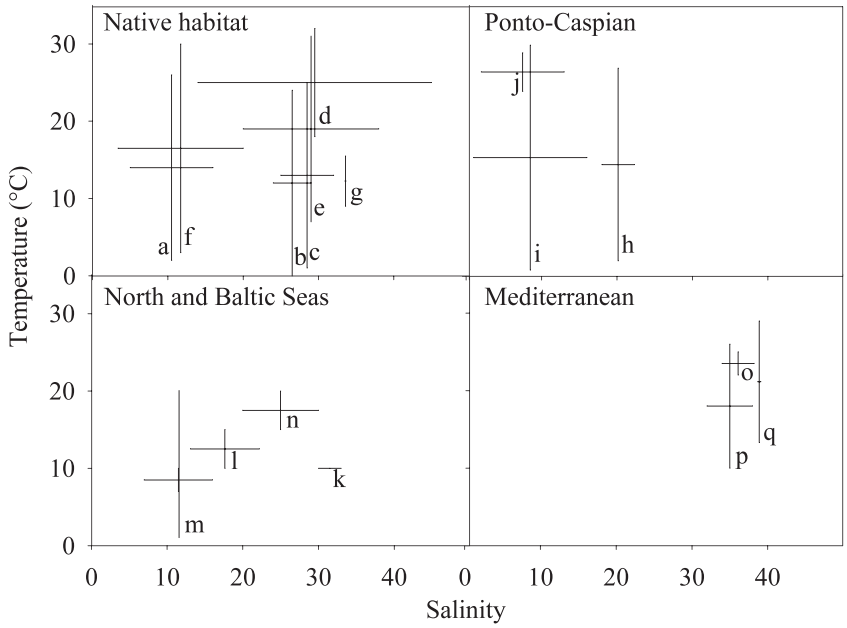

Fig. 1. Observed salinity and temperature ranges in *Mnemiopsis leidyi*'s native and exotic habitats as reported from the native habitat, Ponto-Caspian region, North and Baltic Seas, and the Mediterranean. The letters refer to the studies listed in Table 1.

Baltic Proper (Barz et al. 2006). Previous samplings of *M. leidyi* in the Baltic Proper region have covered limited geographical areas and have reported on the local seasonal variation. A pronounced seasonal abundance pattern seems typical for *M. leidyi* in the Baltic Sea region, with peak adult abundance during autumn or early spring (Javidpour et al. 2009; Riisgård et al. 2010; Schaber et al. 2011). Although *M. leidyi* has shown tolerance to salinities and temperatures typical for the Baltic (Fig. 1; Table 1), the maintenance of a year-round population in the Baltic Proper has been questioned (Schaber et al. 2011).

Here we describe the seasonal dynamics of *M. leidyi* in Skagerrak, Kattegat, and the Baltic Proper and examine how the physical and biological environment shapes its temporal and spatial distribution.

Methods

Sampling program—We conducted monthly sampling of gelatinous plankton and various biological and physical parameters along a transect of eight monitoring stations (1–8) from Skagerrak into the central Baltic Proper (Fig. 2; Table 2). In total, 12 cruises were carried out onboard RV *Argos* from May 2009 until April 2010. An additional 13 stations (A–M) in Skagerrak, Kattegat, and the Baltic Proper were sampled together with the eight monitoring stations during October 2009 onboard RV *Skagerak* (Fig. 2). Also, during December 2009, nine additional stations were sampled in the Gulf of Bothnia (RV *Argos*; Fig. 2). Unless specifically noted, only data from the eight monitoring stations are included in the analyses.

Table 1. References to the studies that proved the observed salinity and temperature ranges of *Mnemiopsis leidyi*'s native and exotic habitat as illustrated in Fig. 1. Letters correspond to letters in Fig. 1.

Region	Letter	Habitat	Reference
Native	a, b, c, d, e	Chesapeake Bay, Long Island Sound, Narragansett Bay, Biscayne Bay, Nueces Estuary	Kremer 1994
	f	Pamlico River Estuary	Miller 1974
	g	Valdés Peninsula (Argentina)	Mianzan et al. 2010
Ponto Caspian	h, i	Black Sea, Sea of Azov	Shiganova et al. 2001
	j	Caspian Sea	Ivanov et al. 2000
North and Baltic Seas	k	North Sea	Boersma et al. 2007
	l	Kiel Bight	Javidpour et al. 2006
	m	Bornholm basin	Huwer et al. 2008
	n	Limfjorden	Riisgård et al. 2007
Mediterranean Sea	o	Catalan Coast	Fuentes et al. 2009
	p	Gulf of Trieste	Shiganova and Malej 2008
	q	Aegean Sea	Shiganova et al. 2001

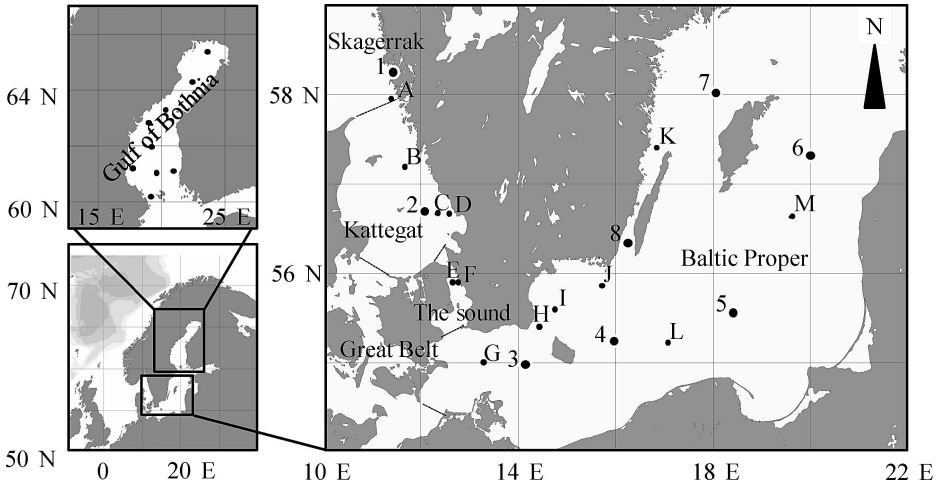

Fig. 2. Stations sampled from May 2009 to April 2010. Sta. 1–8 are monitoring stations sampled monthly (*see* Table 2), Sta. A–M were sampled during October 2009, and the additional nine stations in the Gulf of Bothnia were sampled during December 2009. All stations except C, D, E, and F correspond to SMHI's monitoring stations.

At each station, temperature, conductivity, chlorophyll fluorescence, and oxygen were measured from the surface to near the bottom using a conductivity, temperature, and depth (CTD) Seabird SBE9+ equipped with a SBE 43 oxygen sensor. Water for chlorophyll *a* (Chl *a*) measurements was collected at 5 m intervals from the surface to 20 m followed by 10 m intervals down to 50 m depth. Mesozooplankton were sampled using a WP-2 net with 90 μm mesh size from 25 m to 0 m in the Skagerrak and Kattegat, and from 30 m to 0 m in the Baltic Proper. Samples were preserved with buffered formalin, and organisms were identified and counted under a dissecting microscope. CTD profiles, Chl *a* (uncorrected for phaeopigment), and zooplankton were part of the Swedish Meteorological and Hydrological Institute's (SMHI's) national monitoring program in cooperation with the Swedish environmental protection agency. These data are publicly available at SMHI's Svensk Havsarkiv (SHARK) database. Detailed information on Chl *a* and zooplankton analysis can be found in the Helsinki Commission (HELCOM) manual (http://www.helcom.fi/groups/monas/CombineManual/, accessed May 2009).

Sampling of Mnemiopsis leidyi—Gelatinous plankton were collected using a 300 μm mesh size opening and closing net (Midi MultiNet®, Hydro-bios) with 1.6 L closed cod ends, allowing for five vertically stratified samples within one tow. The net was towed horizontally at 1.8–3.7 km h^{-1}, while slowly being retrieved from the deepest depth to the surface (Table 2). To increase the sampled water volume, the retrieval was regularly stopped at predetermined intervals. The sampled water volume was determined from direct flow meter recordings by the MultiNet (Table 2). Samples were stored at 7°C prior to analysis to avoid degradation of ctenophores. All gelatinous plankton was analyzed live within 1–2 h after collection. Animals > 2 mm were morphologically identified and sized over a transparent backlit table or by the aid of a stereomicroscope. Morphological identification was made for the beroid *Beroe cucumis*, *B. gracilis,* and the cydippid *Pleurobrachia pileus* at all sizes > 2 mm, but was not possible for the early stages of the lobate ctenophores *Bolinopsis infundibulum* and *M. leidyi*. Instead, as adult stages of these species never co-occurred during the same months, the early stages without lobes (approximately 2–6.5 mm) were assumed to correspond to the adult lobate ctenophore present. A subsample of 25 specimens > 2 mm was genetically confirmed as *M. leidyi* (July, August, October, November, December, March) using methods described in Jaspers et al. (2012). Ctenophores < 2 mm caught with a 90 μm net were identified with molecular methods and are reported elsewhere (C. Jaspers and M. Haraldsson et al. unpubl.). Oral–aboral lengths ($L_{o\text{-}a}$) were measured to the nearest mm for ctenophores, and distances between opposite rophalia for scyphomedusae. The remaining zooplankton samples were preserved in 4% buffered formalin. Other gelatinous plankton will be reported elsewhere (M. Haraldsson unpubl).

Data analysis—The integrated abundance (A, individuals [ind.] m^{-2}), mean depth (Z_m, m), and the standard deviation (Z_s, m, which we term the spread below) of the *M. leidyi* vertical distribution were calculated according to Dupont and Aksnes (2012):

$$A = \sum_{i=1}^{n} \Delta Z_i D_i \tag{1}$$

$$Z_m = \frac{\sum_{i=1}^{n} \Delta Z_i D_i Z_i}{A} \tag{2}$$

$$Z_s = \sqrt{\frac{\sum_{i=1}^{n} \Delta Z_i D_i Z_i^2}{A} - Z_m^2} \tag{3}$$

where D_i represents the average *M. leidyi* concentration (ind. m^{-3}) of the sampled depth layer ΔZ_i, Z_i is the mid-

Table 2. Monitoring stations, sampling dates, and depths for the sampling net. NA, not applicable.

Station No.	Position	Total depth (m)	Sampling depth strata (m)					Sampling dates	
			No. 1	No. 2	No. 3	No. 4	No. 5	2009	2010
1	57.52 N 11.18 E	60	0–10*	10–20*	20–30*	30–37*	NA	08 and 29 Jun, 27 Jul, 22 Aug, 14 Sep, 12 Oct, 09 Nov, 10 Dec	17 Jan, 19 Mar, 12 Feb
2	56.40 N 12.07 E	55	0–10*	10–20*	20–29*	NA	NA	12 May, 09 and 30 Jun, 28 Jul, 21 Aug, 15 Sep, 15 Oct, 10 Nov, 09 Dec	18 Jan, 18 Mar, 13 Apr
3	54.58 N 14.05 E	47	0–10*	10–20*	20–29*	NA	NA	12 May, 10 Jun, 01 and 28 Jul, 18 Aug, 16 Sep, 21 Oct, 11 Nov, 08 Dec	19 Jan, 16 Feb, 18 Mar, 14 Apr
4	55.15 N 15.59 E	91	0–10*	10–20*	20–30*	30–50†	50–73†	13 May, 10 Jun, 01 and 29 Jul, 18 Aug, 16 Sep, 18 Oct, 11 Nov, 08 Dec	16 Feb, 17 Mar, 14 Apr
5	55.33 N 18.24 E	90	0–10*	10–20*	20–30*	30–50†	50–73†	13 May, 10 Jun, 01 and 29 Jul, 17 Sep, 16 Oct, 08 Dec	22 Jan, 17 Feb, 16 Mar, 14 Apr
6	57.20 N 20.03 E	240	0–10*	10–20*	20–50‡	50–90§	90–205‖	14 May, 11 Jun, 02 and 30 Jul, 19 Aug, 17 Sep, 17 Oct, 07 Dec	21 Jan, 18 Feb, 16 Mar, 15 Apr
7	58.01 N 17.59 E	205	0–10*	10–20*	20–50‡	50–90§	90–180‖	14 May, 11 Jun, 02 and 30 Jul, 20 Aug, 18 Sep, 17 Oct, 13 and 30 Nov	20 Jan, 15 Mar, 15 Apr
8	56.22 N 16.12 E	21	0–10*	NA	NA	NA	NA	15 May, 12 Jun, 03 and 31 Jul, 20 Aug, 16 Sep, 20 Oct, 14 and 30 Nov	19 Jan, 21 Feb, 15 Mar, 16 Apr

Average filtered water volume (± SD) for: *74 ± 30 m^3; †64 ± 24 m^3; ‡75 ± 26 m^3; §85 ± 27 m^3; ‖145 ± 44 m^3.

depth of each layer i, and n is the number of depth layers (Table 2).

We modeled the probability of *M. leidyi* presence by Generalized Additive Models (GAMs; Hastie and Tibshirani 1986) of the binomial family, using generalized cross validation to find the optimal degree of freedom for each spline smoother (the "mgcv" package; Wood 2006). The dependent variable in all models was presence and absence of *M. leidyi* in depth-pooled data for each station and sampling time, while the independent variables represented either spatio-temporal (ST) positions or environmental (ENV) conditions. Distance from Sta. 1 and week of the year were used as predictor variables in the ST model, and salinity, temperature, and oxygen in the full ENV model. Biotic variables like phyto- and zooplankton abundances were not used in the GAM because *M. leidyi* might affect their prey rather than vice versa, but was instead tested with Spearman's rank correlation against the abundance (ind. m^{-3}) of *M. leidyi*. The simplest GAM model was chosen using stepwise backward elimination. The procedure started with a model containing all predictors, followed by elimination of the least significant predictor ($p > 0.05$), which was repeated until only significant predictors remained. Residual plots and plots of fitted against observed values were used for model evaluation. Since the ST and ENV variables were highly correlated ($r > 0.6$), we partitioned the sources of variation based on a method introduced by Borcard et al. (1992). The basic principle of Borcard et al. (1992) is that the total explained variation can be partitioned into three components: ST variation ([a]), ENV variation ([c]), and variation shared between ST and ENV sources ([b]). Fitted GAM models using ST, ENV, and ST + ENV as predictors will have explained variances equal to [a] + [b], [b] + [c], and [a] + [b] + [c], respectively. From this information, the three variance components ([a], [b], and [c]) can be computed by simple arithmetic expressions (Borcard et al. 1992). The full model (ST + ENV) is part of the partitioning analyses, and should not be interpreted on its own due to the strong correlation between ST and ENV variables. Since our analysis uses a non-normal probability model, we used generalized variances (deviances) in the partitioning calculations, which are expressed as percentage of the total variation, represented by the deviance of a null model without any predictor variables. The resulting deviance partitioning was visualized as a Venn diagram generated by the "VennDiagram" package in R version 2.11.1 (www.r-project.org).

Results

Environmental variables—A strong surface salinity gradient, ranging from 25 to 33 in the Skagerrak to 7 to 8 in the Baltic Proper, was present (Fig. 3). A pronounced halocline existed at all stations, except at Sta. 8. The halocline was generally shallower in the Skagerrak and Kattegat (5–20 m) than in the central Baltic Proper (50–70 m). During February, March, September, and December, larger volumes of saltier water (i.e., salinity > annual average salinity at respective station) were observed at several stations (> 60% of the stations; Fig. 3), indicating

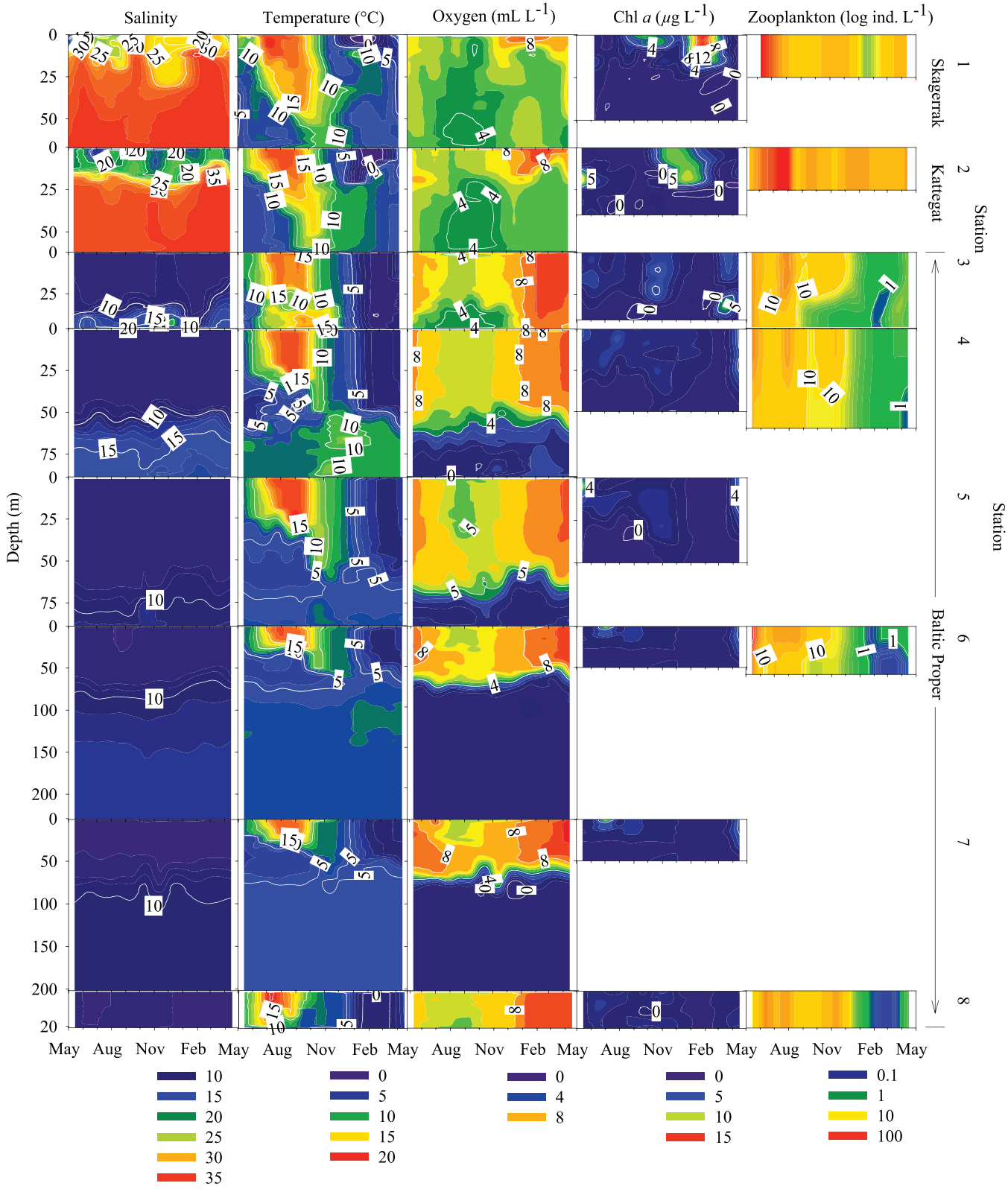

Fig. 3. Contour plots of salinity, temperature (°C), oxygen (mL L^{-1}), Chl *a* (μg L^{-1}), and zooplankton (log ind. L^{-1}) from May 2009 to April 2010 for all monitoring stations. Zooplankton data are missing from Sta. 5 and 7. Note the difference in scale on the y-axis (depth) for Sta. 6 and 7.

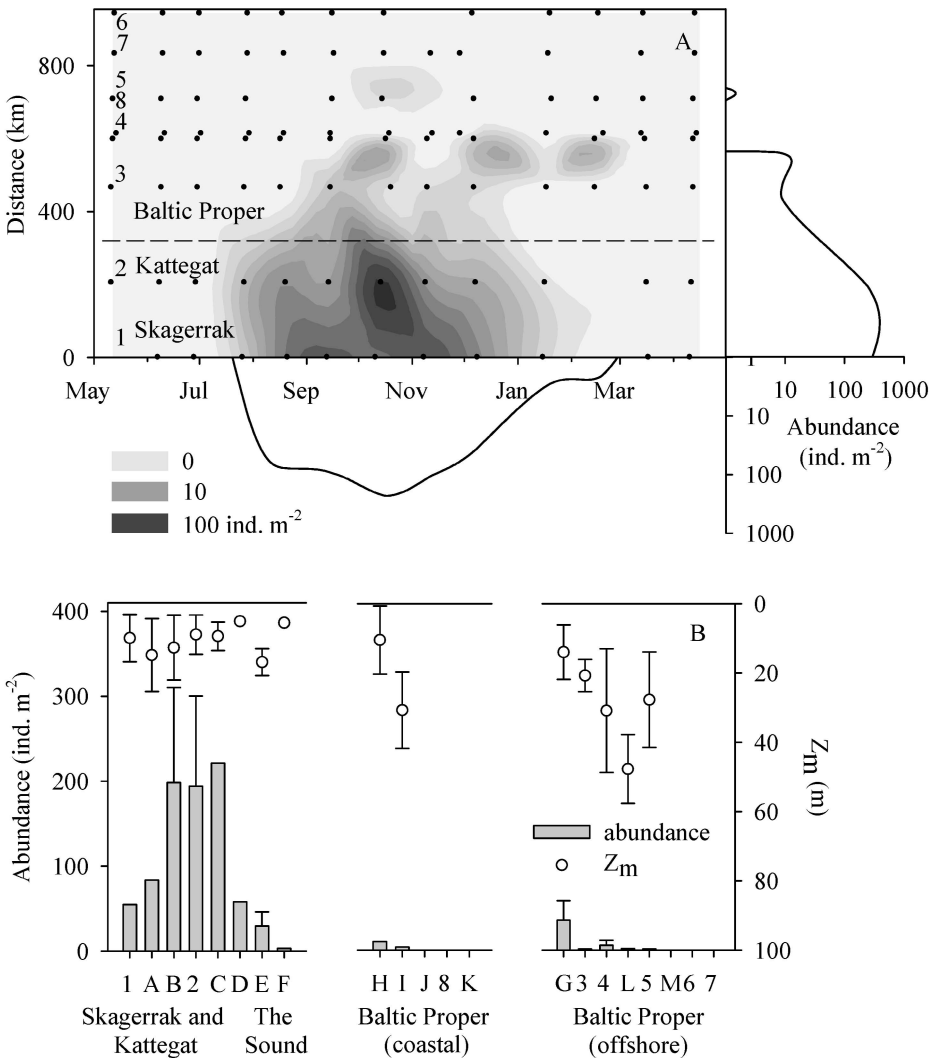

Fig. 4. (A) Abundance of *Mnemiopsis leidyi* (ind. m^{-2}) plotted on log scale against time (month) and distance (nm) from Sta. 1 for the regular monitoring stations, with indicated station numbers (1–8). Every station and occasion sampled is indicated with dots, as some sampling occasions were canceled due to bad weather conditions. The horizontal line represents the border between the Kattegat and the Baltic Proper. (B) Abundance (± SD, ind. m^{-2}) and mean depth ($Z_m \pm Z_s$, m) of *M. leidyi* for stations sampled during October 2009.

an increased deep water inflow from the North Sea into the Baltic Sea. Density profiles generally correlated well with salinity (not shown). Temperature showed strong seasonal changes, and a pronounced thermocline was observed in July–October at 10–20 m in the Skagerrak and Kattegat and at 25–30 m in the Baltic Proper. The winter 2009–2010 was extraordinarily cold, and larger regions than usual were covered with ice from January to March. Oxygen and Chl *a* concentrations varied in parallel with the temperature. Oxygen concentrations were generally high (4.4–9.5 mL L^{-1}), with the exception of a permanent hypoxic layer below 60 m in the Baltic Proper. Chl *a* concentrations peaked in the surface layers in April and November at most of the stations (Fig. 3). Mesozooplankton abundances were highest during late spring and early summer; and, in the Skagerrak and Kattegat, abundances decreased in August. Mesozooplankton abundances in the Baltic Proper were slightly lower, with 10–40 ind. L^{-1} (Fig. 3).

Seasonal and spatial variation in abundance—Throughout the year we found *M. leidyi* at five of the eight monitoring stations (Sta. 1–5; Fig. 4A). Abundances varied with season. *M. leidyi* was continuously present in Skagerrak and Kattegat from July to March, but sporadic in the Baltic Proper between September and February. In the Baltic Proper, *M. leidyi* never extended farther east than Sta. 5, located at the southern Gotland basin (Fig. 2). These patterns were reflected by the ST GAM model. Space and time accounted for 68% of total deviance in the GAM for *M. leidyi* presence (Table 3), with the smoother for location indicating a linear relationship. The average abundances were 60 times larger in Skagerrak and Kattegat

Table 3. Estimated parameters for the ST and ENV GAM models separately and combined (full model). Dev. exp., deviance explained (%); AIC, Akaike information criterion. All variables have a smoothing function.

	Overall model		Model		
Model	Dev. exp.	AIC	Variable	df	*p* value
ST	67.9	43	Time	2.99	0.0044
			Location	1.00	0.0003
ENV	28.6	79	Salinity	2.89	0.0037
			Temperature	1.00	0.0191
			Oxygen	1.00	0.2711
Reduced ENV	29.2	82	Salinity	2.47	0.0003
			Temperature	1.00	0.0360
Full model (ST+ENV; for partitioning analysis)	77.6		Time	2.94	0.0111
			Location	1.00	0.0219
			Salinity	2.95	0.2500
			Temperature	1.00	0.1802

(mean ± SD: 1.16 ± 1.70 ind. m^{-3}) than in the Baltic Proper (0.02 ± 0.04 ind. m^{-3}). Peak abundances occurred in September–October. The highest abundance recorded at a regular monitoring station was 6.69 ± 3.7 ind. m^{-3} at Sta. 2 (Fig. 4A). However, during the extended October cruise abundances of up to 13.4 ind. m^{-3} were recorded in Kattegat at Sta. C, and *M. leidyi* was also found further along the Swedish coast in the southwestern Baltic Proper (Sta. H and I; Figs. 2, 4B). No *M. leidyi* were found in the Gulf of Bothnia during December 2009 (Fig. 2), even

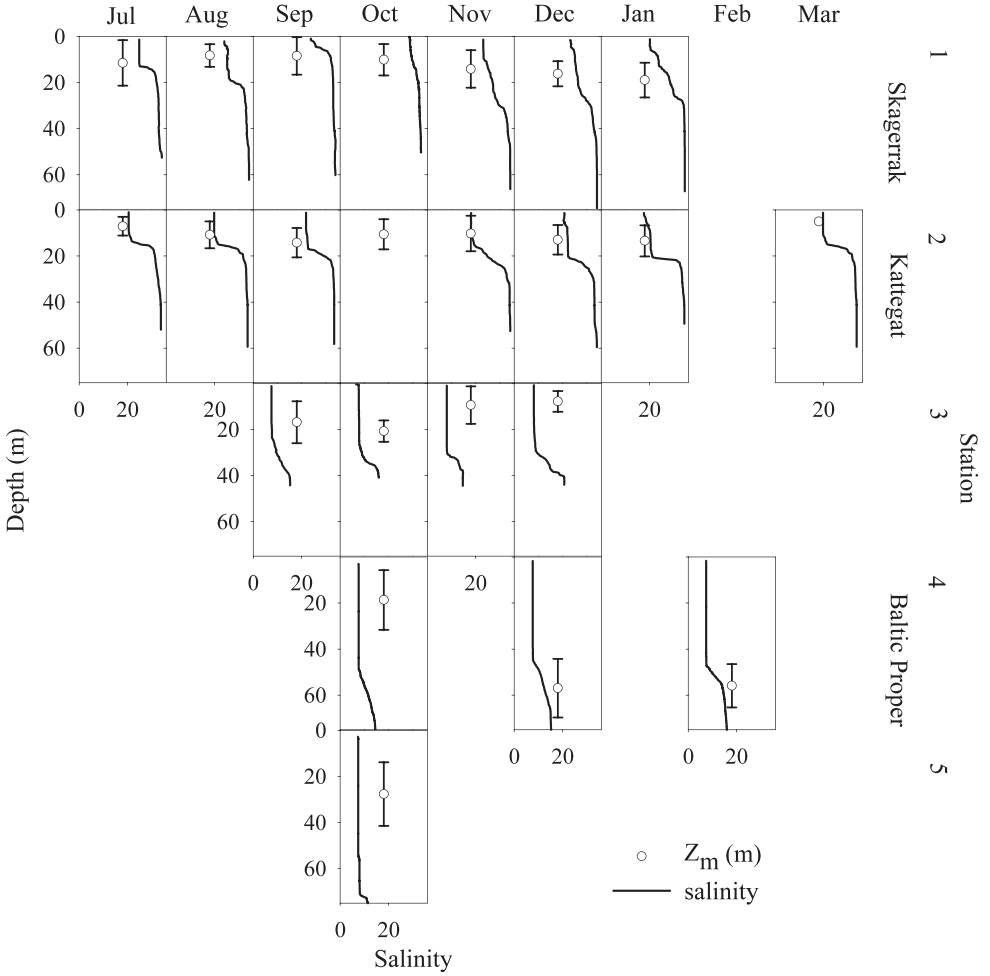

Fig. 5. Mean depth Z_m (± Z_s) of *M. leidyi* and the vertical profiles of salinity for all monitoring stations and months. Note that Z_m is not located according to salinity on the x-axis.

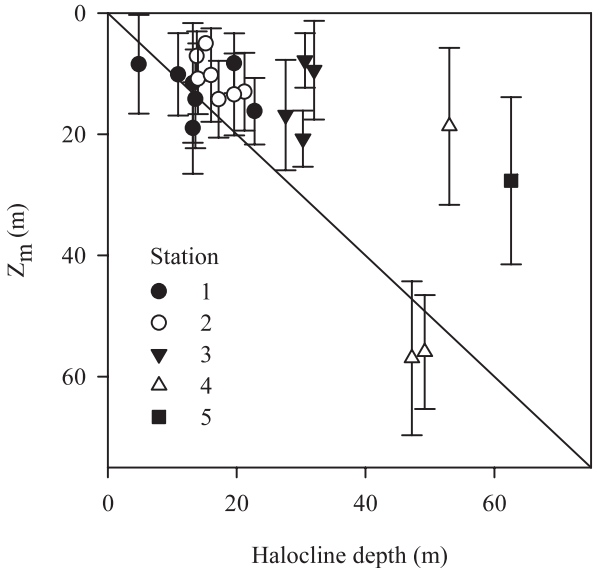

Fig. 6. Mean depth Z_m ($\pm$ Z_s) of *M. leidyi* vs. halocline depth at each station and cruise. The solid line corresponds to the location of Z_m if it was equal to the halocline depth. Dots above this reference line indicate that the mean depth is above the halocline and vice versa.

though *M. leidyi* were present in the southern Baltic Proper (Fig. 2, Sta. 3–4).

Vertical distribution and size—The mean depth (Z_m) of *M. leidyi* was shallower and the vertical spread (Z_s) was narrower in the Skagerrak, Kattegat, and the Sound stations compared to the Baltic Proper stations (Figs. 4B, 5). In Skagerrak, Kattegat, and southwestern Baltic Proper (Sta. 1–3), most individuals were found between 7 and 20 m. In Skagerrak (Sta. 1), individuals were located deeper during the winter months (November–January, Z_m: 14.2–19.0 m) than in July–October (Z_m: 8.4–11.5 m). The opposite pattern was observed in the southeastern Baltic Proper (Sta. 3), with individuals shallower during November–December (Z_m: 7.8–9.4 m) compared to September–October (Z_m: 16.8–20.7 m). Generally, *M. leidyi* was found above the halocline, with the exception of Sta. 4 in the Bornholm basin (Baltic Proper) in December and February (Fig. 6). Also in Skagerrak (Sta. 1), where the halocline was generally very shallow, the mean depth of *M. leidyi* was occasionally located immediately below the halocline (Fig. 6).

The size distribution of *M. leidyi* was wider in the Skagerrak and Kattegat than in the Baltic Proper (Fig. 7). The smaller size classes ($<$ 10 mm) increased during September to December in Skagerrak and Kattegat, while these classes were generally few or lacking at the Baltic Proper stations.

Mnemiopsis leidyi *in relation to the environmental variables*—Most *M. leidyi* were found within a narrow range of salinity, with 80% of the individuals within a salinity of 22–29, salinities typical in the Skagerrak and Kattegat regions (Fig. 8). The distribution was skewed towards the higher salinities of the observed range (Fig. 8). Fifty percent of the individuals occurred within a temperature of 11–16.6°C, and only 10% of the individuals were found at temperatures $<$ 8°C (Fig. 8). Animals were abundant at a wide range of oxygen concentrations (Fig. 8). Most ctenophores were present at Chl *a* levels of 0.7–3.9 μg L^{-1} and mesozooplankton concentrations of 0.13–21.50 ind. L^{-1} (Fig. 8); however, abundance of *M. leidyi* showed no significant correlation with either Chl *a* concentration or zooplankton abundances (Chl *a,* Spearman's rank correlation coefficient $\rho = 0.06$, $p = 0.54$; zooplankton $\rho = 0.04$, $p = 0.76$).

Our final ENV GAM for *M. leidyi* presence suggests that variations in temperature ($p = 0.036$) and salinity ($p = 0.0003$) accounted for 29% of the total variation (the reduced ENV, Table 3; Fig. 9A,B), with a temperature smoother indistinguishable from linear. Oxygen was not significant. The ENV GAM result indicates an optimum habitat (probability of presence > 0.7) at salinities between 12 and 33 and temperatures above 7°C (Fig. 9B). However, the presence of *M. leidyi* was better described by the ST model (Table 3; Fig. 9C) as indicated by the variance partitioning analysis (Fig. 9D). Location and time of the year accounted for 48% of the partitioned deviance in the probability of *M. leidyi* occurrence, while salinity and temperature explained only 10% (Fig. 9D). Twenty-two percent of the total deviance remained unexplained in the full model (ST + ENV).

Discussion

M. leidyi is known to tolerate a wide range of environmental conditions both in its native and exotic habitat (Fig. 1; Table 1), which indicates that *M. leidyi* could survive in the Baltic Sea. Still, whether *M. leidyi* can maintain a year-round population has been questioned (Schaber et al. 2011), and experimental work suggests salinity constraints on *M. leidyi* in the Baltic Proper (Jaspers et al. 2011). Our data, covering large parts of the Skagerrak, Kattegat, and Baltic Proper during 1 yr, agree with a salinity-constrained population and suggest that the Baltic Sea population is maintained through advection and depends on yearly reintroduction from source areas.

Temperature, prey, and predator conditions have earlier been suggested as the main factors controlling native *M. leidyi* populations (Kremer 1994; Purcell et al. 2001), while salinity has been regarded as a less important factor. In the invaded Ponto-Caspian region, low salinities only seem to limit the population during low temperatures (Shiganova et al. 2001). In contrast, egg production of *M. leidyi* from the Baltic Proper, both in situ and in laboratory experiments, has been shown to decline with decreasing salinities (salinity interval 6–33; Jaspers et al. 2011), such that the low salinity (< 9) surface water of the Baltic Proper may limit population growth. Thus, the environmental range required for successful recruitment and establishment appears to be much narrower (Figs. 8, 9B) than that tolerated by *M. leidyi* (Fig. 1; Table 1). This is reflected in the narrow optimum vs. the total range of the environmental variables, which is particularly evident for salinity

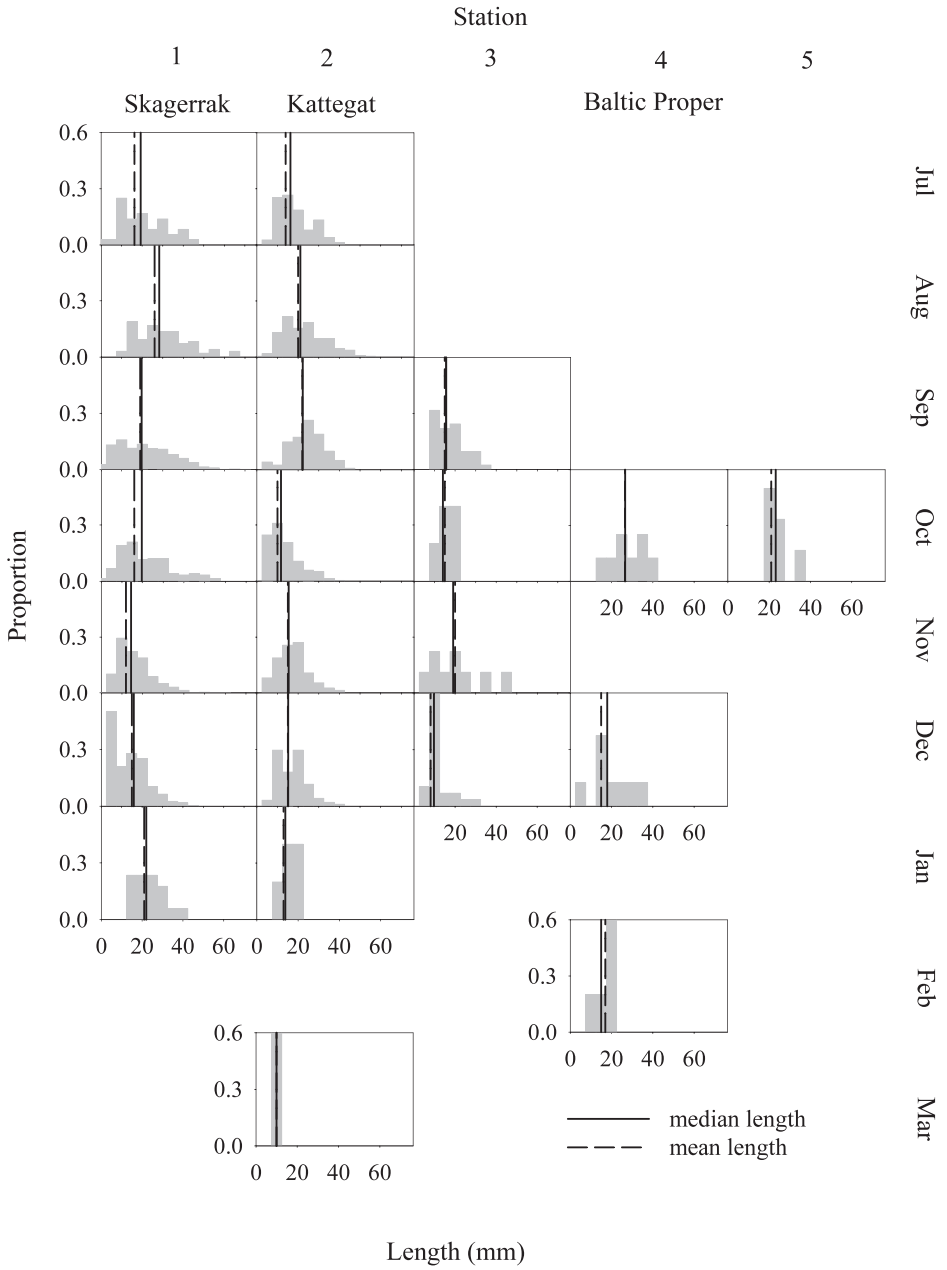

Fig. 7. Length histogram of *M. leidyi* for each station and cruise.

(Fig. 8), and in the skewed occurrence towards higher temperatures.

Our GAM models suggested environmental restrictions (e.g., salinity and temperature) on the sampled population, but ST factors seemed to have the strongest influence on the observed distribution pattern. The presence of *M. leidyi* as predicted by the ENV conditions suggested a rather narrow salinity range, which gets narrower with decreasing temperatures (Fig. 9B). However, given the deviance partitioning analysis, 2/3 of the variation accounted for by temperature and salinity could just as well be accounted for by ST variation, while the variation in the ST variables uniquely accounted for 40% of the total variation. One interpretation is that this relatively high share of the total variation reflects transport of individuals by advection, which brought *M. leidyi* outside its preferred temperature and salinity range.

There are several indications that *M. leidyi* have been transported into the Baltic Proper. (1) Average abundances were up to 60-fold higher in Skagerrak and Kattegat compared to in the Baltic Proper. (2) The appearance in the Baltic Proper was generally delayed and more sporadic (Fig. 4). (3) Smaller individuals were underrepresented in the Baltic Proper (Fig. 7), implying reduced reproduction and/or high mortality rate for the smaller size classes (C. Jaspers and M. Haraldsson et al. unpubl.), which suggests unsuccessful local recruitment in the Baltic Proper and supports recruitment through advection rather than by reproduction.

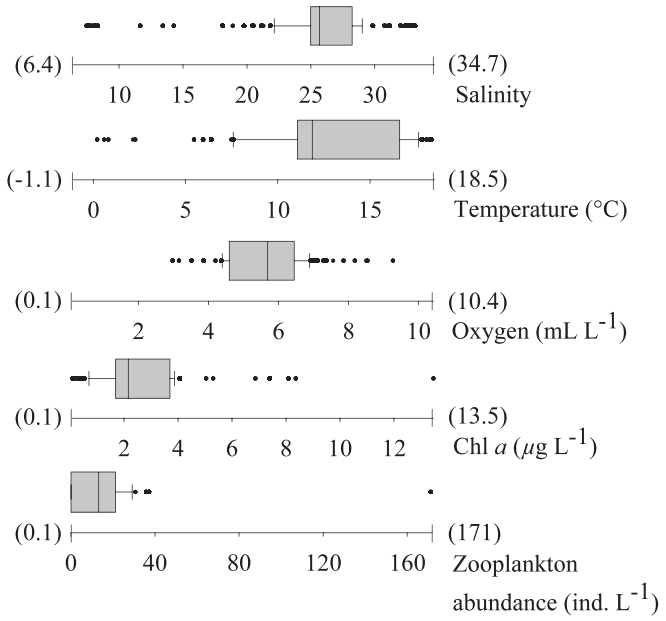

Fig. 8. Distributions of environmental variables at locations where *M. leidyi* was found. Variables have been averaged over the depth interval sampled for *M. leidyi*. The box represents 50% of all observations, with the solid line representing the median, the whiskers 10th and 90th percentiles, and the dots outliers. Axes scales correspond to minimum and maximum averages of measured variables over the sampled depth interval at all locations. The box plots are based on 3634 observations.

(4) Transportation of *M. leidyi* into the Baltic Proper is also suggested by the association of *M. leidyi* with deeper, high-salinity water at several of the stations in the Baltic Proper (Sta. 4–5; Figs. 4B, 5, 6). Huwer et al. (2008) and Schaber et al. (2011) also reported higher densities of *M. leidyi* around the halocline (40–60 m) in the Bornholm basin. Variation in the inflow of North Sea water into the Baltic Sea depends on variation in climatic forcing (Reissmann et al. 2009), and this may affect the transportation of organisms into the Baltic Sea (Barz et al. 2006). In addition, the ctenophore *Bolinopsis infundibulum*, a typical North Sea species (Hansson 2006), was also caught in deeper water at Arkona in May 2009 (M. Haraldsson unpubl.), indicating the possibility of transportation from the North Sea via Skagerrak and Kattegat. Alternatively, the association with deeper and more saline water might reflect avoidance of the shallower brackish water.

Source and sink dynamics, as indicated by our data, have also been reported for *M. leidyi* in native temperate regions where, e.g., winter temperatures fall below the threshold for reproduction (Costello et al. 2006). It has been suggested that source populations are located in protected coastal regions during periods of low abundance and that they seed other regions during favorable conditions (Costello et al. 2006). However, these overwintering regions often have low salinities (Costello et al. 2012), in contrast to the pattern between salinity and temperature tolerance that we observed in the Baltic (Fig. 9C). Invaded habitats have also shown source–sink dynamics. In the low-saline Sea of Azov, the invasive *M. leidyi* cannot survive the winter temperatures and gets reintroduced via the Black Sea each year (Shiganova et al. 2001). Likewise, in Limfjorden in Northern Europe, an overwintering population has not been observed since its introduction, and the animals are likely reintroduced from the North Sea (Riisgård et al. 2012). Other regions, like the northern Caspian Sea, act only as sink regions during years with very cold winter temperatures (Shiganova et al. 2001). Similarly, animals observed in the Baltic Proper may have been transported via the Skagerrak and Kattegat from the North Sea, where salinities are higher, or from local regions around the Kiel Bight or Kerteminde fjord, where extreme abundances have been observed occasionally (Javidpour et al. 2009; Riisgård et al. 2010). Based on genetic diversity, Reusch et al. (2010) suggested an initial introduction in the Baltic Proper with possible further transportation into the North Sea. Although our data from 2009–2010 do not support this transportation route, overwintering and possible source regions may differ between years, depending on the environmental conditions for that year, in a similar fashion as in the northern Caspian Sea (Shiganova et al. 2001). Costello et al. (2006) proposed that seasonal persistence throughout the year should define a source population for holopelagic species such as *M. leidyi*, because traditional demographical parameters, such as natality, mortality, immigration, and emigration, are difficult to estimate for such species.

The apparent differences in environmental tolerance of *M. leidyi* between regions (Fig. 1) may reflect different genotypes. Genetic analyses have revealed that the southern Ponto-Caspian *M. leidyi* originate from the southern native habitat in the Gulf of Mexico (Fig. 1, region e), while the North Sea and Baltic Proper populations stem from the northern native habitat (i.e., Woods Hole and Narragansett Bay, Fig. 1, region c; Reusch et al. 2010). This might suggest that southern and northern populations have different environmental requirements (cf. Fig. 1), and that the probability of a new establishment increases if the introduced individuals originate from similar environmental conditions (Reusch et al. 2010). However, successful invaders generally display a large genotypic plasticity, which allows them to quickly adapt to new environments (Lee 2002). If *M. leidyi* can maintain a population in the region of the Baltic Proper, which lies on the limit of their environmental tolerance (Fig. 1, region m), it might evolve an increased tolerance for this new habitat.

In conclusion, the low salinity of the Baltic Proper appears to constrain local recruitment of *M. leidyi* and the survival of a year-round population, and transport of individuals by advection from source areas outside the area, presumably the North Sea, appears to be the main cause for the observed Baltic Proper occurrences. Thus, repeated future introductions by means of the regular advection of saline water into the Baltic Proper must be expected.

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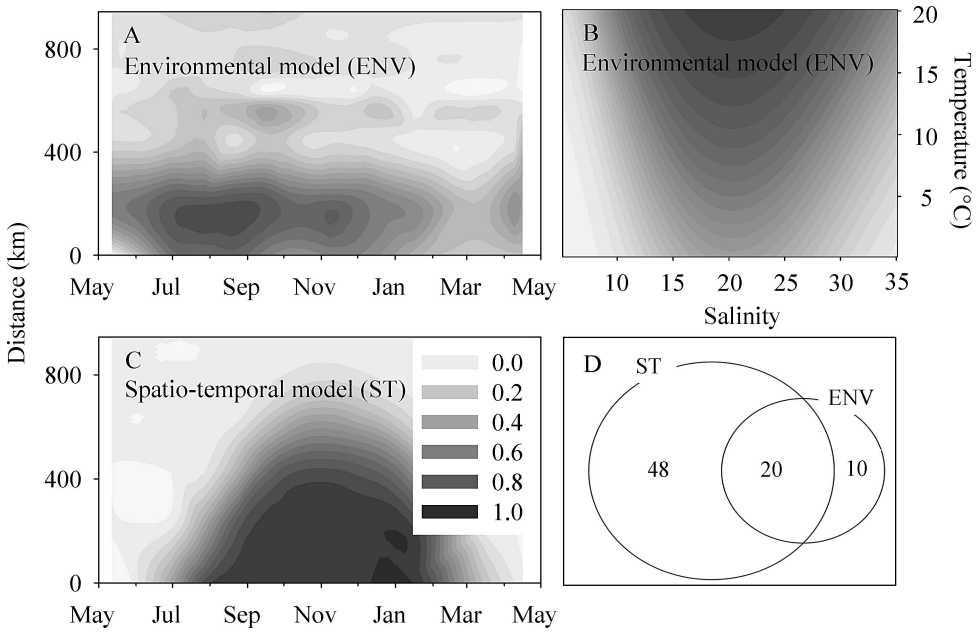

Fig. 9. Probability of *M. leidyi* presence predicted by the ENV GAM model (*see* Table 3) in relation to (A) the month of the year and the distance from Sta. 1 in Fig. 2 given the observed average temperature and salinity in the region and (B) given salinity and temperature intervals. (C) The probability of *M. leidyi* presence predicted by the ST GAM model (*see* Table 3) in relation to the month of the year and distance from Sta. 1. (D) The partitioning of deviance (%) explained by the ST and ENV models. The shared explained variation was 20%, and the residual variation 22%.

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